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Density-Dependent and Density-Independent Factors Influencing Reproductive Rates in Northwest Atlantic Harp Seals, *Pagophilus groenlandicus.*

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Obtaining accurate estimates of reproductive rates are critical for estimating the population dynamics of a species. Recent estimates of late term pregnancy rates, fecundity and abortion rates of Northwest Atlantic harp seals were obtained from samples collected off the coast of Newfoundland and Labrador. The declining, but highly variable, reproductive rates reported previously have continued with the pregnancy rate of mature females (2010 and 2011; <0.3) falling to the lowest level since data was first collected in the 1950s. Using a fixed-dispersion, beta regression model to explore the importance of biological and environmental conditions, we found that reproductive rates were influenced by both density dependent and independent factors. While the general decline in fecundity is a reflection of density-dependent processes associated with increased population size, including the late-term abortion rates captured much of the large inter-annual variability. Changes in the annual abortion rate could be described either by a model that incorporated ice cover in late January or a model that incorporated ice cover and capelin biomass obtained from the previous fall as a proxy for prey availability. Using these models, we predicted the 2012 fecundity rate to be 0.44 or 0.54, depending upon the model used which is lower than the estimate (0.643) obtained from the small sample of reproductive tracts.

Key words: harp seal, *Pagophilus groenlandicus*, reproductive rates, fecundity, abortions, density dependent, density independent, beta model.

Facteurs dépendants et indépendants de la densité qui ont une incidence sur les taux de reproduction du phoque du Groenland (*Pagophilus groenlandicus*) de l'Atlantique Nord-Ouest

RÉSUMÉ

Il est essentiel d'obtenir des estimations précises des taux de reproduction pour évaluer la dynamique de la population d'une espèce. De récentes estimations du taux de gestation tardive, de fécondité et d'avortement des phoques du Groenland de l'Atlantique Nord-Ouest ont été obtenues à partir d'échantillons prélevés sur la côte de Terre-Neuve-et-Labrador. La tendance des taux de reproduction à la baisse, mais très variables, enregistrés précédemment, se poursuit avec un taux de gestation des femelles adultes (moins de 0,3 en 2010 et 2011), se classant au niveau le plus bas depuis la collecte des premières données dans les années 1950. À l'aide d'un modèle de régression bêta et de dispersion fixe pour étudier l'importance des conditions biologiques et environnementales, nous avons constaté que les taux de reproduction ont été influencés par les deux facteurs dépendants et indépendants de la densité. Le déclin général de la fécondité reflète les processus qui dépendent de la densité associée à l'effectif de la population croissant, y compris les taux d'avortement au dernier trimestre qui représentent bien la grande variabilité interannuelle. Des changements pour ce qui est des taux d'avortement annuels pourraient être décrits par un modèle qui intègre une couverture de glace à la fin du mois de janvier ou un modèle qui intègre les données liées à la couverture de glace et à la biomasse du capelan obtenues l'automne précédent à titre d'indicateur de la disponibilité des proies. À l'aide de ces modèles, nous avons prévu le taux de fécondité de 0,44 ou 0,54 en 2012, selon le modèle utilisé, ce qui est inférieur à l'estimation (0,643) obtenue à partir du petit échantillon des voies génitales.

Mots-clés : phoque du Groenland, *Pagophilus groenlandicus*, taux de reproduction, fécondité, avortements, dépendance à la densité, indépendant de la densité, modèle bêta.

INTRODUCTION

Understanding fecundity is critical for determining population dynamics and predicting future changes. Population dynamics are influenced by changes in fecundity that are the result of a complex interaction between intrinsic factors related to changes in population (i.e. density dependent) and extrinsic factors involving environmental variability (i.e. density independent) (e.g. Eberhardt 1977, Gaillard et al. 2000, de Little et al. 2007). However, determining the relative importance of these different factors is difficult for most species as they require extensive, long term, measurements of reproductive rates, population and a variety of environmental factors. This particularly difficult for migratory species that may encounter varying conditions in different parts of their range.

The harp seal (*Pagophilus groenlandicus*) is an abundant, migratory species distributed throughout most of the North Atlantic. The Northwest Atlantic population summers primarily in the Arctic waters of eastern Canada and western Greenland (Sergeant 1991; Stenson and Sjare 1997). In the fall, harp seals migrate southward to overwinter and pup on the pack-ice off the coast of northeast Newfoundland and southern Labrador, or in the Gulf of St. Lawrence during late February or early March. Breeding occurs once the pups are weaned, after which seals one year of age and older undergo their annual moult. Following a brief period of feeding, the seals migrate northward to the summering areas.

Female reproductive tracts have been collected from harp seals in Newfoundland and southern Labrador waters since the 1950s, with a more systematic program initiated in the 1980s that continues today (Sjare and Stenson 2010). Bowen et al. (1981) observed that as the population declined during the 1950s and 1960s, the mean age of sexual maturity declined from approximately 6.2 y in 1952 to 4.5 y in 1979, while the pregnancy rate of mature females increased from 85 to 95 %. Bowen et al. (1981) considered it likely that density-dependent mechanisms were involved, but emphasized that sufficient empirical data were still lacking. Sjare and Stenson (2010) evaluated changes in the reproductive parameters of female harp seals up to 2004. They found that pregnancy rates subsequently declined to 65 to 70 % by the early 1990s and varied between 45 and 70 % from 2000 to 2004. Concurrently, the mean age at sexual maturity decreased from 5.8 (SE = 0.02) years in the mid-1950s to 4.1 (SE = 0.02) in the late 1970s, increased to 5.5 (SE = 0.03) years by the early 1990s, and peaked at 5.7 (SE = 0.01) in 1995. From 2000 to 2004, mean age at sexual maturity varied from 4.9 (SE = 0.01) to 6.0 (SE = 0.01) years. Although the direction of changes they observed is consistent with a density-dependent response, changes in population size explained relatively little of the variability observed. At the same time, dramatic changes in the Northwest Atlantic ecosystem have occurred suggesting that other ecological or environmental factors have an important influence on reproductive rates (McLaren et al. 2001; Drinkwater 2004; Sjare and Stenson 2010). Stenson and Wells (2011) extended this dataset with data from 2004 through 2008; they found that the trends observed by Sjare and Stenson (2010) had continued with reproductive rates generally continuing to decline but with high inter-annual variation. For example, late term pregnancy rates of mature females varied from a low of 40 % in 2004 to 75.3 and 73.8 %, in 2007 and 2008, respectively.

Harp seals must build up energy reserves that can be used during the breeding periods. Chabot and Stenson (2002) found that male harp seals returned from their high-latitude feeding grounds heavier, in better condition, and with a thicker blubber layer than when they left the area the previous spring. However, maxima in length, mass, condition and blubber thickness were not observed until immediately before the whelping period in late February, or in the case of seals younger than 5 year, sometime in March. A similar trend was observed in females; a significant proportion of the energy used during reproduction was attained during the winter period when

they were off the coast of Newfoundland (Chabot and Stenson, unpublished data). Therefore, changes in prey availability in the southern portion of their annual range are likely to have a major impact on the ability of females to complete a pregnancy successfully.

The Northwest Atlantic harp seal population is the target of large commercial and subsistence hunts in Canada and Greenland (Stenson 2010), and is managed primarily by quotas on the Canadian commercial hunt which take into account reported catches and other sources of mortality (DFO 2008). These quotas are based upon estimates of population size and predictions of future trends obtained from a population model that incorporates information on removals and annual estimates of age-specific reproductive rates with independent estimates of pup production by adjusting the starting population and adult mortality to fit a time series of pup production estimates (e.g. Hammill et al. 2011, 2012). Understanding the changes that have occurred in reproductive rates and the factors that control them is critical to estimate total abundance and to predict the future impact of hunting and climate change.

The objective of this study is to update the analyses presented in Stenson and Wells (2011) including data on age-specific pregnancy rates up to 2013. Using these data, we explore the influence of density-dependent and independent factors on the reproductive rates in northwest Atlantic harp seals.

METHODS

REPRODUCTIVE RATES

Data to 2008 were taken from Stenson and Wells (2011) although the data for 2008 were updated. The data and methods of collection are summarized in Sjare and Stenson (2010) and Stenson et al. (2009). Female reproductive tracts and jaws were collected from harp seals collected around Newfoundland and southern Labrador since 1979. Sampling has focused upon a core area along the northeast coast of Newfoundland which is adjacent to key winter and spring feeding habitat. Samples were collected by experienced seal hunters and Department of Fisheries and Oceans (DFO) personnel under licenses issued by DFO. To minimize potential sampling biases among years, a core group of hunters from different areas of the province obtained a sample of seals over the entire period. Reproductive tracts were either preserved in 10 % formalin or frozen in the field; in the laboratory, ovaries were cut into 2.0 mm thick serial sections for examination.

Ages were determined to the nearest year by sectioning a lower canine tooth and counting dentine annuli (Fisher 1954; Bowen and Sergeant 1983, Fire et al. 2011). Females were considered immature if the ovaries were small and contained only inactive follicles with no *corpus luteum* (CL) or *corpus albicans* (CA) (Fisher 1954; Bowen et al. 1981). If there was evidence of a CL and/or CA in either ovary, the seal was considered mature. Mature females were considered pregnant if the ovary contained a large, fully luteinized CL in one of the ovaries and, since 1985, the presence of a foetus. Mature non-pregnant females lacked an active CL, but showed evidence of having ovulated previously (i.e., a CA was present). As in previous studies, all seals less than three years of age were immature (Sjare and Stenson 2010).

For ovaries collected after 1984, the size of all CA and CL were measured in two directions and the mean recorded. For ovaries prior to 1985, the maximum diameter was recorded. Seals that lacked a developing foetus, but had a CL $\geq$ 13 mm or CA $\geq$ 12 mm, a ruggose uterus and a large uterine horn, were assumed to have pupped recently. For seals collected prior to February 15th, it was assumed that those pups did not survive and that this represented a late term abortion. For seals collected after February 15th, was assumed that there was a high probability that these pups would have survived.

Fecundity rates, defined as the proportion of mature females that are pregnant, and age specific pregnancy rates were calculated as per Sjare and Stenson (2010). Late term pregnancy and fecundity rates were estimated from seals collected between October and February.

MODELLING FACTORS AFFECTING FECUNDITY

The Data

Biological rates

The late-term pregnancy rate of mature females in a given year (referred to as fecundity rate) was based on samples taken between October and February (Sjare and Stenson 2010).

Annual abortion rate was defined as the proportion of mature females collected before February 15th in a given year that showed signs (defined above) of having recently aborted.

Population

Abundance of Northwest Atlantic harp seals was obtained from a model that incorporates information on annual estimates of age specific pregnancy rates, commercial and subsistence catches in Canada and Greenland, an estimate of the number of seals killed but not landed, by-catch in commercial fishing gear in Newfoundland and the United States, and mortality of young seals due to poor ice conditions, to determine the population trajectory (Hammill et al 2011). The model was fit to twelve periodic estimates of pup production from 1952 to 2012 by adjusting initial population size and natural mortality. The model incorporates density-dependent function acting on young of the year survival and assumes a carrying capacity of 12 million. The model is described by Hammill et al (2011) although the input data has been extended to 2012.

Ice area cover

As a proxy for habitat change we used the percentage ice area cover on January 29 of each year. The percentage ice cover was defined as the proportion of the regional East Coast (Area: 1975854 km^2) that was covered by first year ice ($\geq$ 30 cm thickness). These data are available annually from 1969 through 2013 from the Canadian Ice Service.

As a proxy for the prey field harp seals encounter while the embryo is developing, we derived relative biomass indices for three common prey species: capelin (*Mallotus villosus*), sand lance (*Ammodytes americancus*) and Arctic cod (*Boreogadus saida*) from DFO's fall bottom trawl survey (Stenson 2012; Koen-Alonso *et al.* 2010; McCallum and Walsh 1996). The prey data begins in 1995, as prior to then the fishing gear used (Engels trawl) had low catchability for small fish. Because it is not possible to correct the earlier data for many of the species eaten by harp seals, we used data since 1995 when DFO began using a Campelen trawl during the fall bottom-trawl survey.

The Analysis

Given that rates assume values in the standard unit interval (0; 1), we modelled pregnancy and abortion rates using fixed-dispersion, beta regression models (Cribari-Neto and Zeileis 2010). This approach incorporates features such as heteroskedasticity or skewness, commonly observed in data such as rates or proportions (Cribari-Neto and Zeileis 2010). All analyses were performed using the betareg package (Cribari-Neto and Zeileis 2010) in R (R Development Core Team 2012).

Pregnancy rates of mature females (Fecundity)

Given the different lengths of the time series available, we broke this analysis into two separate components. In the first component we modelled fecundity rate as a function of those variables for which we had long-term data, i.e. population size, abortion rate, fecundity rate the previous year and ice coverage. The effect of population size on fecundity rate represents density-dependent effects. The potential effect of habitat is expressed through the variable ice coverage. Abortion rate would negatively affect fecundity rate. The rationale for including fecundity rate the previous year was that if fecundity rate was low females might potentially be in better condition the following year and it would enhance the probabilities of taking the pregnancy to term. Thus, the model had the form (using a log link):

$$\text{fecundity rate}_t \sim \text{population size}_t + \text{abortion rate}_t + \text{ice coverage}_t + \text{fecundity rate}_{t-1}$$

We built all possible candidate models (without including interactions) and ranked and selected the best model based on the Akaike Information Criterion corrected for small sample sizes(AICc) (Burnham and Anderson 2002) and the derived measure evidence ratio (E_i) (Anderson 2008).

Once model selection was completed we kept the variables that we found to provide the most parsimonious description of fecundity rates and tried to improve the fit of the model by incorporating the effects of prey availability during the previous fall. For this second component of the analysis we could only use data since 1995, given the length of the prey field data series. Therefore, this model had the form (using a log link):

$$\text{fecundity rate}_t \sim \text{variables from analysis 1} + \text{capelin biomass}_{t-1} + \text{sandlance biomass}_{t-1} + \text{arctic cod biomass}_{t-1}$$

To select the most parsimonious model, we followed the same strategy as in the first component of the analysis.

Abortion rate

We modelled abortion rate as a function of the available habitat, prey availability the previous fall and abortion rate the previous year. We hypothesize that abortion rate the previous year could have a negative effect on abortion rate, i.e. if abortion rate is high in any given year seals would potentially be in better condition the next year and avoid abortions. Thus, the model had the form (using a log-log link):

$$\text{abortion rate}_t \sim \text{ice coverage}_t + \text{abortion rate}_{t-1} + \text{capelin biomass}_{t-1} + \text{sandlance biomass}_{t-1} + \text{arctic cod biomass}_{t-1}$$

We employed the same strategy to select the most parsimonious model as we did for the fecundity rate analysis.

Assessment of the impact of sample size on the variability of fecundity rates

To assess the impact of sample size on the variability of fecundity rates, we conducted a simulation analysis. We bootstrapped (random sampling with replacement from the original dataset) individual seals at different resampling intensities (from 5 to 100 individuals in increments of 5 seals). We used data from recent years when the sample size was greater than 100 individuals (i.e. 2006, 2009-2011, Table 1). We drew 10,000 bootstrap resamples each year at each resampling level. We calculated the fecundity rate from each bootstrap resample, and calculated the variance across bootstrap resamples.

RESULTS

REPRODUCTIVE RATES

Age-Specific Pregnancy Rates

Sampling effort has varied throughout the sampling period, with large numbers of animals collected in some years, while in others considerably fewer were obtained (Table 2). Generally, sample sizes for seals 8 years of age and older (8+) have been greater than 30, although samples were smaller in the early 1980s and then in 2012 (n=28) and 2013. Sample sizes for younger seals are quite small in most years throughout the time series.

Because of the small sample sizes, there is no new data on pregnancy rates for seals less than 8 years of age. As described previously (Sjare and Stenson 2010; Stenson and Wells 2012), pregnancy rates for 3 year olds were very low. Among the 4 and 5 year olds, reproductive rates were higher during the late 1970s and early 1980s than in earlier years. Since the mid 1980s pregnancy rates have declined to the lowest in the time series. Pregnancy rates for 6 year olds were low (< 67 %) since the mid 1990s when compared with earlier years when rates averaged around 80 %. 7 year old seals also had relatively low pregnancy rates from 2002-2008 when compared with earlier years, with the lowest year on record being 2005 (17 %). No 7 year olds have been sampled since 2008.

Among the 8+ animals, pregnancy rates were high (80–90 %) until the mid 1980s, Pregnancy rates declined in the late 1980s although sample sizes in the mid 1980s were small which makes it difficult to determine exactly when the change occurred. Since then, pregnancy rates have fluctuated greatly but with a declining trend. In the past decade, 8+ pregnancy rates have average approximately 55 %. During 2004, a survey year, only 38 % of the seals were pregnant while in 2008, another survey year, the rate was the highest since 1990 (77.2 %). Since then, pregnancy rates dropped dramatically to a low of only 20 % in 2011 (Table 2). The estimate of pregnancy rate in 2012 was much higher (64 %), and the preliminary estimate for 2013 is even higher (83 %), but these estimates are based upon small sample sizes (e.g. only 6 in 2013).

Fecundity and Abortion Rates

The estimated fecundity and abortion rates are shown in Table 1. The criteria for identifying late term abortions was based upon the observed diameters of CL and CA in seals identified as being pregnant with implanted embryos. Very few CL with a mean diameter of less than 13 mm were observed in pregnant seals collected during January and February (Figure 1). Therefore, the presence of a large CL (>13 mm) with no implanted foetus in January or early February indicated a female that had dropped her pup prematurely.

Following birth, the diameter of the CA declines rapidly (Figure 2). Peak pupping off Newfoundland occurs between the 7th and 10th of March. Within a month, the mean diameter of the largest CA regresses to, in general, less than 10 mm. Thus, females with a CA diameter greater than 12 mm do not represent a pregnancy from the previous year and are likely to have terminated their pregnancy within the previous 30 days. The majority of females that were considered to have aborted were identified as such based upon the presence of a large CA and ruggose uterus; the remainder were identified based upon the presence of a CL in the absence of a foetus.

Until the late 1970s, more than 85 % of the mature females were pregnant each year. Since then fecundity rates have been highly variable, but with a declining trend (Table 1, Figure 3a). The lowest rate in the time series occurred in 2011 (20.9 %) while the rates in 2007 and 2008 (75.3 and 73.8 %, respectively) were some of the highest seen in recent years.

No late term abortions were detected in females collected prior to 1987 (Table 1). Since then, abortions appear to have occurred in almost every year although the rate varies greatly. Generally, the rate of abortion appeared to be higher in years with lower overall fecundity (Figure 4). For example, the highest abortion rates (0.238 and 0.233) occurred in 2004 and 2010 which were years with some of the lowest fecundity rates.

FACTORS INFLUENCING FECUNDITY AND ABORTION RATES

Fecundity Rate

The data used to model factors influencing fecundity rates are shown in Figure 3. Using the long term data series, the most parsimonious model to describe the fecundity rate included population size and abortion rate as explanatory variables. This model had almost 66 times the empirical support relative to the second best model ($E_{min,i}$=65.93), which included only population size as explanatory variable (Table 3). The model that includes only population size as explanatory variable captures the general decrease in fecundity that started during the 1980s (pseudo R^2 ($R_p^2 = 0.49$)). However, there is a large amount of variability around the general decreasing trend that the model fails to capture (Figure 5). When abortion rate is included in the model, this variability is captured ($R_p^2 = 0.83$). All relationships were negative.

Thus, for the second part of the analysis we kept population size and abortion rate as explanatory variables with a shortened time series but added prey availability to see if they improve the model fit. Although the relative biomass of Arctic cod marginally improves model fit ($R_p^2 = 0.83$ vs $R_p^2 = 0.81$, Figure 6), the most parsimonious model only included population size and abortion rate. This model had 6.27 the weight of evidence relative to the model that incorporated the biomass of arctic cod the previous fall (Table 1). Patterns of variation in fecundity rates were well captured by the model with population size and abortion rate as explanatory variables, particularly during 2000-2010 (Figure 6).

Abortion Rate

Abortion rates were best described by the model that included only ice coverage in late January as explanatory variable, although it was practically indistinguishable from the model that also included the availability of capelin the previous fall (Table 3). The relationships between abortion rate and ice, or ice and capelin, were negative. All models that can be considered to have reasonable empirical support included ice coverage and one or more terms of prey availability the previous fall (capelin and/or Arctic cod). In addition, one model that can be considered plausible contains a term for abortion rate during the previous year ($E_{min,i}$=6.77). The two most parsimonious models showed a reasonably good fit to the abortion rate data ($R_p^2 = 0.51$ and $R_p^2 = 0.67$), although there were 4 years during the early 2000s when the models did not behave as expected (Figure 7).

Predictions

To estimate the abortion and fecundity rates in 2012, we fit the models to data until 2011. From the most parsimonious models (abrate$_t$ ~ ice coverage$_t$ and abrate$_t$~ ice coverage$_t$ + capelin biomass$_{t-1}$) we predicted 2012 abortion rates ($\widehat{ar_{2012}}$). We then used these predicted abortion rates as inputs to our best fecundity rate model. We predicted $\widehat{ar_{2012,ice}} = 0.24$ and $\widehat{ar_{2012,ice+cap(t-1)}} = 0.12$. (Figure 8). Using these rates we predicted fecundity rates of 0.44 and 0.54, respectively (Figure 9). The fecundity rate observed was 0.64 with no abortions, although this estimate is potentially unreliable due to the low sample size (n=28) available.

Impact of Sample Size on the Variability of Fecundity Rates

The variance of fecundity rate is an exponentially decreasing function of sample size (Figure 10). The variance shows a very steep decline as sample size increases, until reaching sample sizes of around 40-50 seals when the curve becomes asymptotic (Figure 10).

DISCUSSION

The highly variable, but generally declining reproductive rates observed by Sjare and Stenson (2010) and Stenson and Wells (2011) have continued. In fact, the pregnancy rate of mature females fell to the lowest in the time series in 2010 and 2011. These data suggest that the population may be exhibiting density-dependent changes due either to increasing population densities or declining resources (i.e. declining resources per capita). Over the past decade, however, the population has been relatively stable (Hammill et al. 2012). Sjare and Stenson (2010) attempted to correlate changes in mean age of maturity with population size, but found that population size could not explain much of the variation over the entire time series. They concluded that other ecological or environmental factors are also impacting the population.

We were able to explore the importance of several biological and environmental conditions, and found that fecundity rates were influenced by both density-dependent and independent factors. While the general decline in fecundity is a reflection of density-dependent processes associated with increased population size, including the late term abortion rates into the model captured much of the large inter-annual variability.

It is to be expected that the availability of food would have a direct impact on the ability of a female to carry a pregnancy to full term (e.g. Eberhardt 1977, Gaillard et al. 2000, de Little et al. 2007). However, we found that ice conditions in late January (i.e. over a month prior to pupping), were also important; as ice declined the abortion rates increased. Seals may be responding to years when ice does not appear to be forming up normally for pupping, but ice conditions may also be a proxy for other ecosystem conditions that affect the condition of the seals. Buren et al (2014) found that capelin biomass and spawning are correlated with ice conditions in the northwest Atlantic. The annual cycle of seasonal ice cover in this area have a variety of other ecosystem impacts that we have not identified as of yet.

The addition of capelin biomass had a slight impact on the model fit. Given the importance of capelin as prey for harp seals (Lawson et al. 1995, Lawson and Stenson 1997, Stenson 2012), it is surprising that it did not have more of an effect. Unfortunately, however, we do not have robust estimates of capelin biomass (DFO 2013). The estimates we used here were obtained from the DFO fall groundfish survey. As a pelagic species, bottom trawl surveys are not the best tool to assess capelin because of their poor catchability (O'Driscoll et al. 2002), but they may provide a useful proxy for general trends in biomass over time. Many of these same issues could apply to our estimates of Arctic cod and sand lance biomass. Improved estimates of all three species' biomass, and trends, would allow us to improve our understanding of the influence changes in prey availability are having on abortion rates.

The occurrence of a significant number of late term abortions has not been reported before. Occasionally white-coated harp seal pups have been reported or observed during research trips during the winter (Stenson, pers. obs). However, they have been relatively few. In January 2011, however, local hunters and fishery officers reported a large number of pups on the beaches near Nain, in northern Labrador. The pups were abandoned and all were reported to have died. We estimated that approximately 13 % of the mature females in our sample aborted in 2011 and that similar, or higher, proportions had occurred previously (2010, 2009, 2006, 2004 and 1989). Large numbers of premature pups were not reported during the early years, but

unlike 2011 when ice was very limited (Stenson and Hammill 2012), shore ice was more extensive in these years and, given the tendency of harp seals to remain with the pack ice, few people were offshore to look.

The abortion rates we estimated are likely minimums. The majority of cases we identified were based upon the presence of a large CA and ruggose uterus. Given how quickly CA regress, females that aborted more than one month prior to sampling could not be separated from females that gave birth the previous spring. Also, we assumed that females still carrying foetuses would successfully carry out the pregnancy to full term and would not have aborted later. It is possible that some of the pups that were born late in the pregnancy may have survived but the number of females sampled later in February was not large and, based upon the CA size, did not appear to have pupped recently.

Given the highly variable annual pregnancy rates, obtaining accurate estimates is critical for assessing this population. Hammill and Stenson (2011) found that using annual estimates of reproductive rates for older age classes (8+) was necessary in order to understand the large differences observed between the 2004 and 2008 pup production estimates. The population model could not fit to the two estimates when using smoothed pregnancy rates that assumed the variation among years was primarily due to sampling error (e.g. Stenson et al. 2009). Another pup production survey was carried out in 2012 that resulted in a much lower estimate of pup production than in 2008 (Stenson et al. 2014). The estimated fecundity in 2012 (0.64) is only slightly lower than seen in 2008 (0.70) and no abortions were identified. However, sample sizes were quite small in 2012; shore based hunters were unable to get many seals in either 2012 or 2013 and reported that very few animals were in the area. Based upon the models developed here, we predict that some abortions would have occurred in 2012 and that fecundity would be lower (0.44 or 0.54) than the available samples suggest. The difference between the two predictions is due to the influence of the high capelin biomass estimated in fall 2011 which resulted in a lower estimate for the model that included ice conditions only.

An initial estimate of fecundity in 2012, based upon 20 samples, was 0.70 (Hammill et al. 2014). The inclusion of only a few additional samples, however, reduced this estimate substantially. This suggests that the current sample may not be a true reflection of fecundity in 2012 and illustrates the importance of obtaining an adequate number of samples, particularly of older females, to estimate annual reproductive rates. Based on the simulation exercise we carried out, a minimum sample size of 40 to 50 mature females should be obtained annually so as to diminish the effects of sample size on our estimates of reproductive rates.

The data we have presented here indicates that, generally, reproductive rates of northwest Atlantic harp seals have continued to decline. Some of this decline may be explained by changes in population, but the decline has continued in recent years when the population has been relatively stable, suggesting the importance of environmental factors that are influencing the occurrence of late term abortions. Along with prey availability, poor ice conditions, either as a direct influence on pupping habitat or as a proxy for other ecosystem changes, appears to be correlated with rate of abortions. Ice conditions have also been shown to have an impact on capelin abundance through a match-mismatch mechanism in timing of the annual primary productivity bloom (Buren et al 2014). Although the North Atlantic has undergone periods of relative cooling and warming, even within recent times, overall the trend has been for warmer temperatures and deterioration in ice conditions (Johnston et al. 2005, Friedlaender et al. 2010, Bajzak et al. 2011). Climate change models predict that this warming trend will continue (McCarthy et al. 2001, IPCC 2007, Walsh 2008). If so, it is likely that reproductive rates will remain, on average, relatively low and unlikely to respond in a proportional density dependent manner. Therefore, it is important to be conservative when predicting how reproductive rates will respond to changes in abundance in the future.

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TABLES

Table 1: Annual late-term fecundity (# pregnant / # mature) and abortion (# abortions / # mature) rates of female harp seals, October through February, 1954 – 2013. 2013 rates are preliminary.

Year	# Mature Females	Fecundity Rate	Abortion Rates
1954	51	0.863	0
1964	32	0.844	0
1965	161	0.925	0
1966	59	0.983	0
1967	163	0.988	0
1968	85	0.929	0
1969	187	0.968	0
1970	116	0.948	0
1978	88	0.943	0
1979	51	0.941	0
1980	14	0.786	0
1981	29	0.862	0
1982	9	0.778	0
1985	10	0.700	0
1986	10	0.900	0
1987	44	0.705	0.023
1988	26	0.769	0.038
1989	31	0.806	0.129
1990	14	0.571	0.071
1991	36	0.694	0.028
1992	55	0.655	0.073
1993	47	0.468	0085
1994	60	0.767	0.033
1995	36	0.667	0.083
1996	38	0.684	0
1997	42	0.762	0.119
1998	44	0.636	0.023
1999	80	0.563	0.025
2000	54	0.704	0.019
2001	42	0.667	0.048
2002	93	0.505	0.108
2003	95	0.663	0.053
2004	80	0.300	0.238
2005	95	0.611	0.011
2006	119	0.479	0.143
2007	89	0.730	0.034
2008	61	0.705	0.033
2009	105	0.562	0.124
2010	116	0.293	0.233
2011	148	0.209	0.128
2012	28	0.643	0
2013	6	0.833	0

Table 2. Age specific pregnancy rates of female harp seals sampled in Newfoundland and Labrador waters during October to late February from 1954 to 2013. Rates are based on the proportion of pregnant females in a particular age class regardless of maturity status. 2013 rates are preliminary.

Age	3			4			5			6			7			8		
Year	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate
1954	4	0	0	3	1	0.333	3	2	0.667	16	12	0.750	4	3	0.750	29	26	0.897
1964	11	0	0	9	1	0.111	2	1	0.500	4	3	0.750	5	5	1.000	20	17	0.850
1965	30	1	0.033	44	5	0.114	37	20	0.541	38	27	0.711	33	28	0.848	76	68	0.895
1966	7	0	0	9	1	0.111	17	6	0.353	11	8	0.727	8	7	0.875	41	36	0.878
1967	10	0	0	19	4	0.211	33	20	0.606	29	28	0.966	3	20	0.870	100	89	0.890
1968	27	0	0	19	6	0.316	20	14	0.700	12	11	0.917	11	9	0.818	44	39	0.886
1969	25	1	0.040	25	4	0.160	16	7	0.438	28	23	0.821	9	27	0.931	136	119	0.875
1970	13	0	0	13	3	0.231	12	6	0.500	10	9	0.900	19	18	0.947	88	74	0.841
1978	40	1	0.025	38	23	0.605	20	18	0.900	9	6	0.667	10	7	0.700	31	28	0.903
1979	21	5	0.238	15	8	0.533	5	5	1.000	9	8	0.889	4	4	1.000	7	16	0.941
1980	2	0	0	2	1	0.500	1	1	1.000	0	0	-	2	2	1.000	10	7	0.700
1981	5	1	0.200	4	3	0.750	2	1	0.500	7	6	0.857	0	0	-	17	14	0.824
1982	4	0	0	5	2	0.400	1	1	1.000	4	3	0.750	0	0	-	3	1	0.333
1985	4		0	3	1	0333	5	2	0.400	3	3	1.000	0	0	-	1	1	1.000
1986	1	1	1.000	0	0	-	2	1	0.500	1	0	0	1	1	1.000	6	6	1.000
1987	12	2	0.167	8	3	0.375	9	7	0.778	4	4	1.000	1	1	1.000	23	14	0.609
1988	17	2	0.118	6	1	0.167	3	3	1.000	0	0	-	3	2	0.667	16	12	0.750
1989	8	0	0	9	0	0	6	2	0.333	3	2	0.667	2	2	1.000	20	20	1.000
1990	8	0	0	7	1	0.143	3	1	0.333	1	0	0	0	0	-	10	6	0.600
1991	10	0	0	11	2	0.182	7	4	0.571	3	1	0.333	3	1	0.333	26	17	0.654
1992	10	2	0.200	11	3	0.273	9	4	0.444	8	6	0.750	2	2	1.000	30	19	0.633
1993	11	1	0.091	17	2	0.118	7	0	0	5	4	0.800	3	2	0.667	32	15	0.469
1994	23	1	0.043	16	2	0.125	14	6	0.429	7	3	0.429	5	5	1.000	36	29	0.806
1995	10	0	0	13	6	0.462	4	2	0.500	5	2	0.400	0	0	-	24	14	0.583
1996	8	0	0	6	0	0	4	1	0.250	1	1	1.000	0	0	-	35	24	0.686
1997	6	0	0	4	0	0	10	3	0.300	2	2	1.000	2	1	0.500	34	26	0.765
1998	6	0	0	10	3	0.300	9	2	0.222	4	2	0.500	9	6	0.667	27	16	0.593
1999	6	0	0	7	0	0	18	4	0.222	15	6	0.400	9	7	0.778	50	30	0.600
2000	1	0	0	9	3	0.333	6	4	0.667	5	2	0.400	6	3	0.500	37	26	0.703
2001	2	0	0	0	0	-	2	2	1.000	3	0	0	3	3	1.000	36	23	0.639
2002	2	0	0	4	1	0.250	5	3	0.600	17	10	0.588	7	4	0.571	65	36	0.554
2003	1	0	0	3	2	0.667	2	1	0.500	3	2	0.667	4	2	0.500	87	57	0.655

Age	3			4			5			6			7			8		
Year	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate	n	No Preg	Preg Rate
2004	2	0	0	5	0	0	5	1	0.200	1	0	0	8	5	0.625	68	26	0.382
2005	9	1	0.111	9	0	0	13	2	0.154	7	0	0	6	1	0.167	80	54	0.675
2006	2	0	0	0	0	-	0	0	-	0	0	-	5	3	0.600	114	64	0.561
2007	1	0	0	5	0	0	3	1	0.333	2	2	1.000	2	1	0.500	82	63	0.768
2008	6	0	0	3	0	0	2	0	0	0	0	-	4	1	0.250	57	44	0.772
2009	1	0	0	1	0	0	1	0	0	1	1	1.000	0	0	-	103	57	0.553
2010	3	0	0	0	0	-	0	0	-	1	0	0	0	0	-	116	34	0.293
2011	3	0	0	2	1	0.500	0	0	-	0	0	-	0	0	-	147	30	0.204
2012	1	0	0	1	0	0	1	0	0	0	0	-	0	0	-	28	18	0.643
2013	0	0	-	0	0	-	0	0	-	0	0	-	0	0	-	6	5	0.833

Table 3. Model selection statistics for the fecundity and abortion rates analyses. The delta Akaike Information Criterion corrected for small sample sizes (Δ AICc) and the derived measure evidence ratio (Emin,i) for each model are included. We only show models with an Emin,i smaller than 10.

Analysis	Model	$\Delta AICc_i$	$E_{min,i}$
Fecundity rate Analysis 1	fecundity rate$_t$ ~ population size$_t$ + abortion rate$_t$	0.00	1.00
	fecundity rate$_t$ ~ population size$_t$ + abortion rate$_t$ + fecundity rate$_{t-1}$	8.38	65.93
Fecundity rate Analysis 2	fecundity rate$_t$ ~ population size$_t$ + abortion rate$_t$	0.00	1.00
	fecundity rate$_t$ ~ population size$_t$ + abortion rate$_t$ + arctic cod biomass$_{t-1}$	3.67	6.27
Abortion rate	abortion rate$_t$ ~ ice coverage$_t$	0.00	1
	abortion rate$_t$ ~ ice coverage$_t$ + capelin biomass$_{t-1}$	0.16	1.08
	abortion rate$_t$ ~ ice coverage$_t$ + arctic cod biomass$_{t-1}$	1.37	1.98
	abortion rate$_t$ ~ ice coverage$_t$ + capelin biomass$_{t-1}$ + arctic cod biomass$_{t-1}$	2.49	3.47
	abortion rate$_t$ ~ ice coverage$_t$ + abortion rate$_{t-1}$ + capelin biomass$_{t-1}$	3.82	6.77

FIGURES

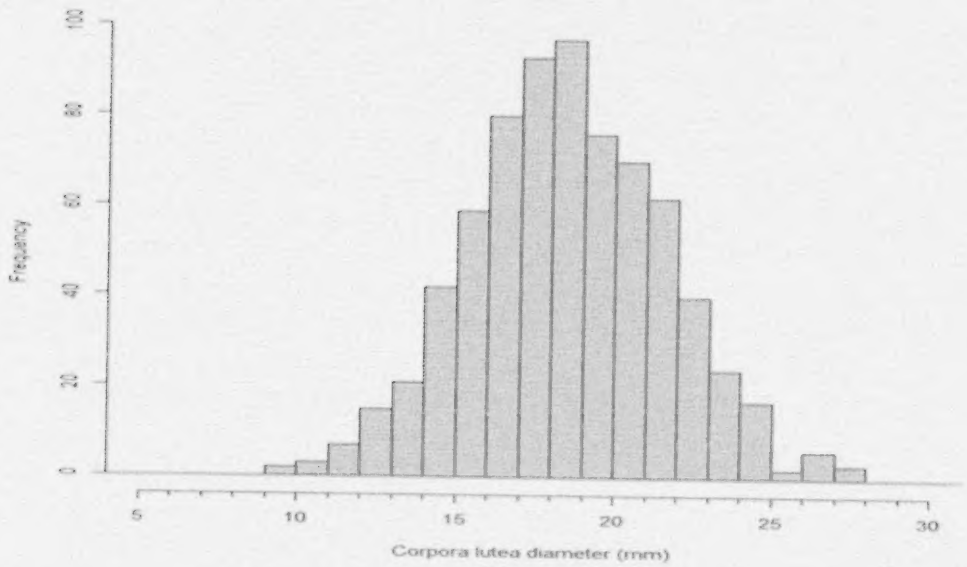

Figure 1. Mean diameters of corpora lutea (mm) present in pregnant harp seals November through February.

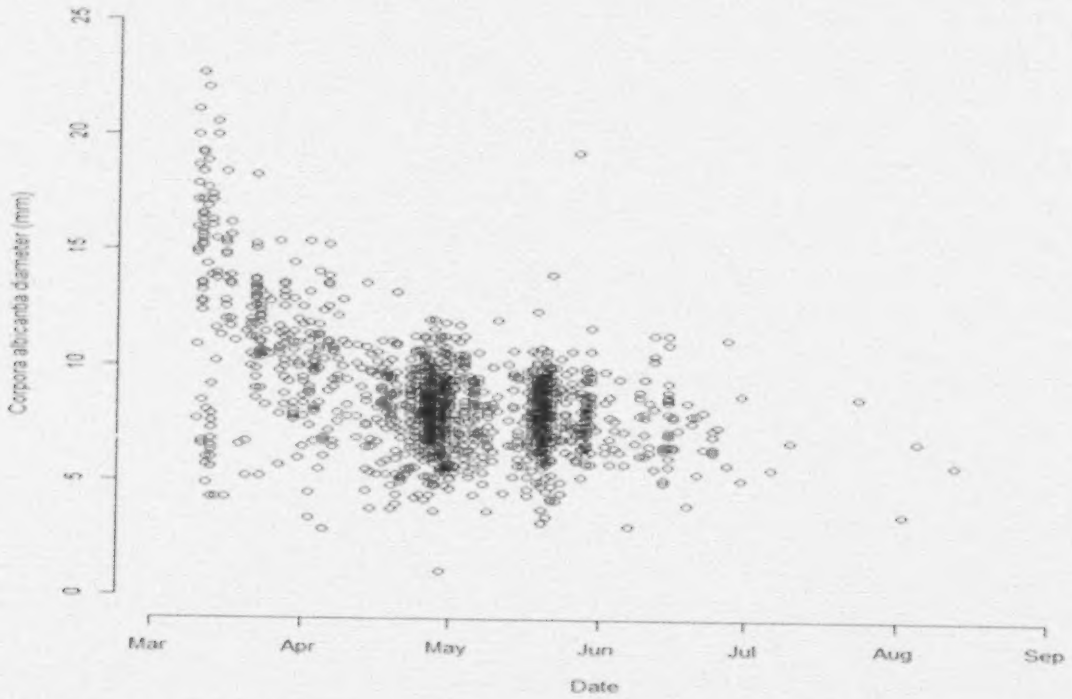

Figure 2. Mean diameters of corpora albicantia (mm) present in female harp seals following birth showing the rapid regression in diameter of the corpora. Data are shown starting on 10 March.

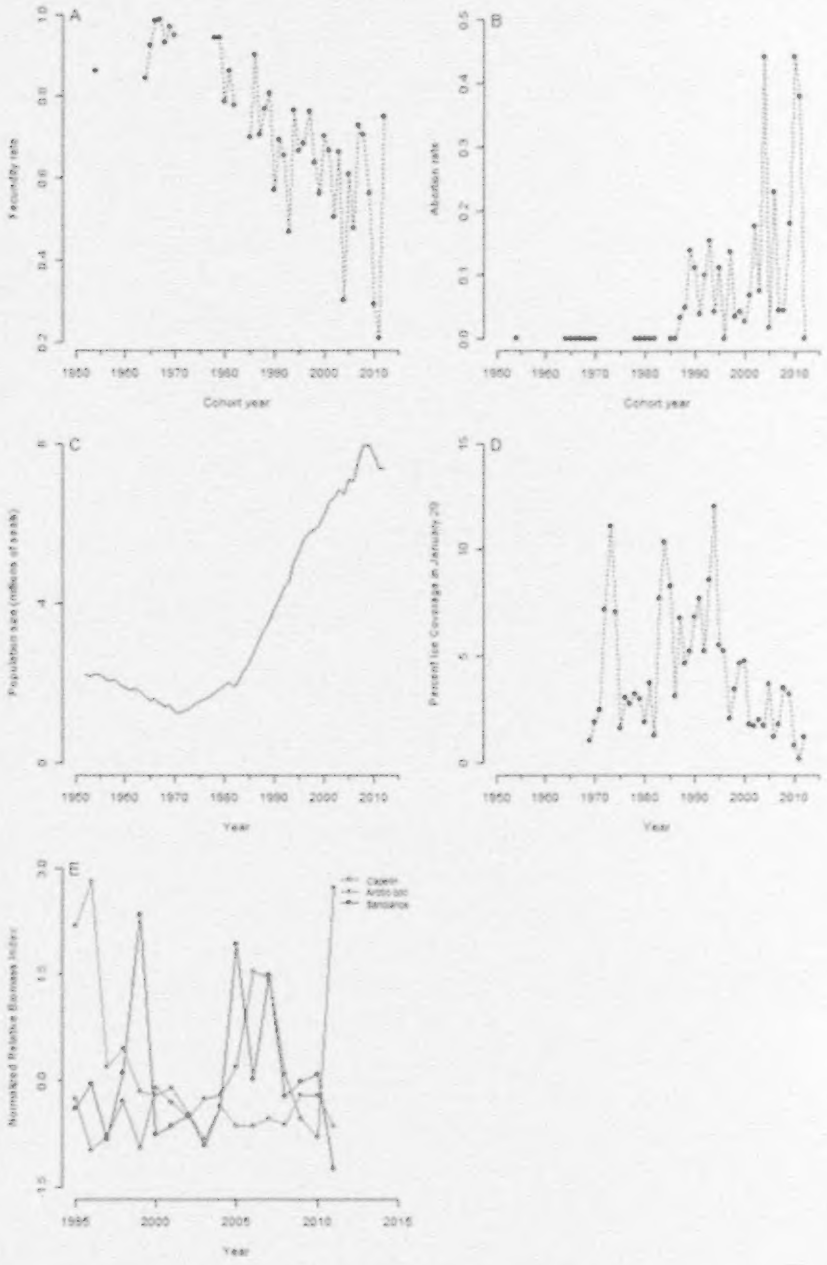

Figure 3. Data used in the fecundity and abortion rates analyses. A. Fecundity rate, B. Abortion rate, C. Harp seal population size, D. Percent ice coverage of the Canadian East Coast in January 29, E. Normalized relative fall biomass indices of capelin, arctic cod and sandlance.

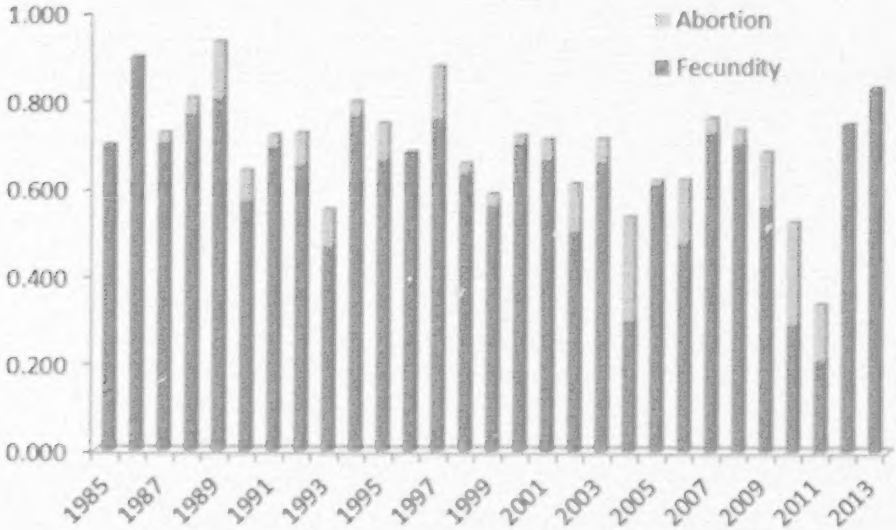

Figure 4. Proportion of mature females collected in December through mid-February that were pregnant or showed indications of having aborted their foetus wihtin the past month. 2013 rates are preliminary.

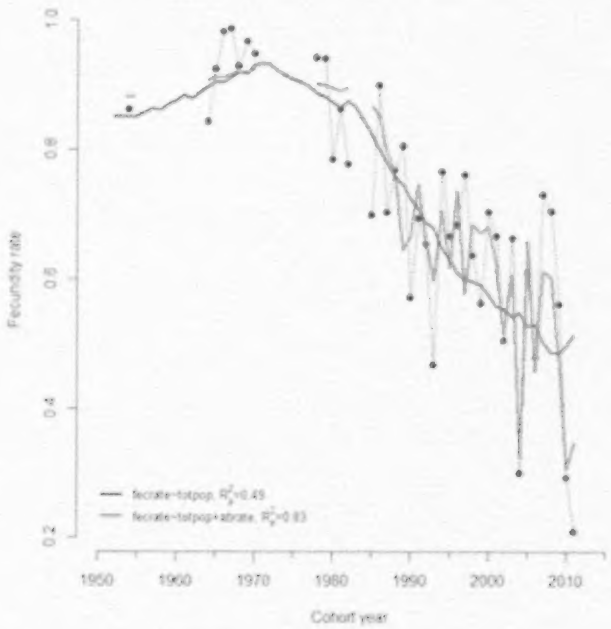

Figure 5. Fits of the two most parsimonious models to describe fecundity rate, based on the long-term data series, 1952-2011.

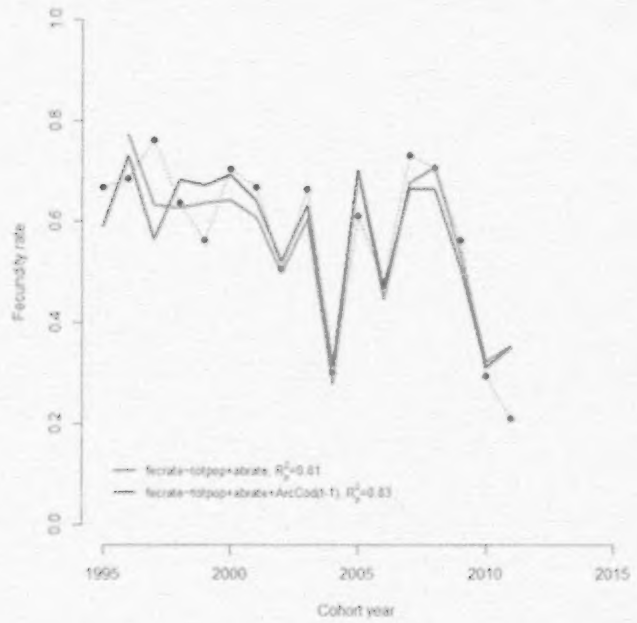

Figure 6. Fits of the two most parsimonious models to describe fecundity rate, when incorporating the effects of prey availability using data 1995-2011.

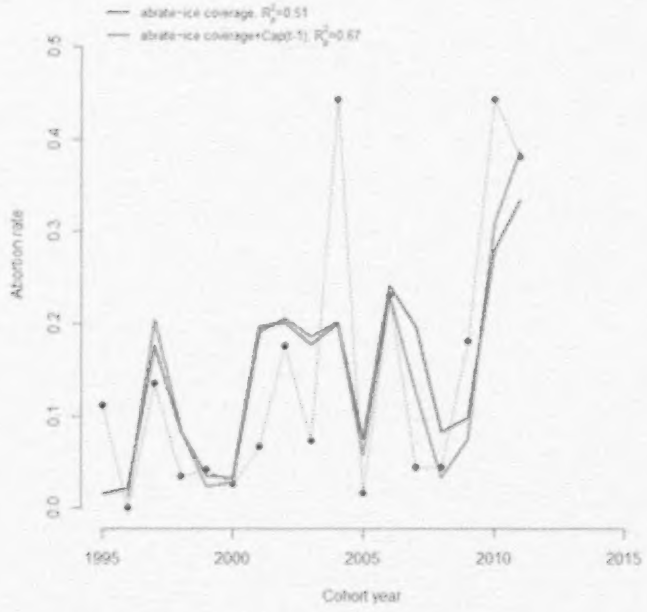

Figure 7. Fits of the two most parsimonious models to describe abortion rate using data from 1995-2011.

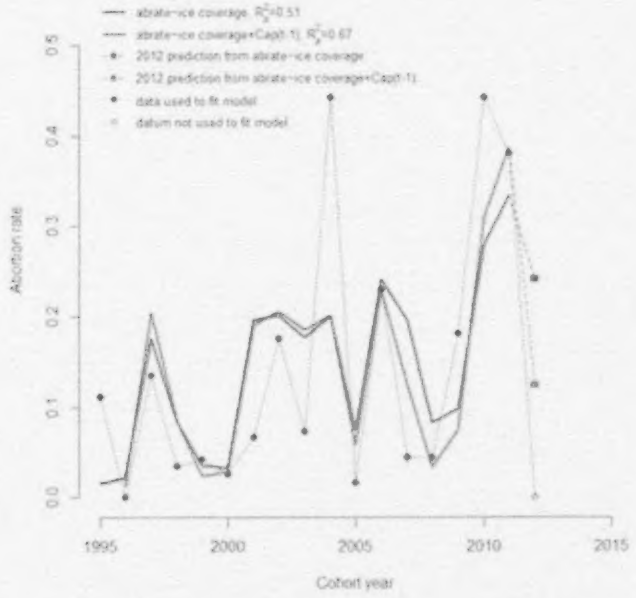

Figure 8. Predictions of the 2012 abortion rate from the two most parsimonious models based upon data from 1995-2011.

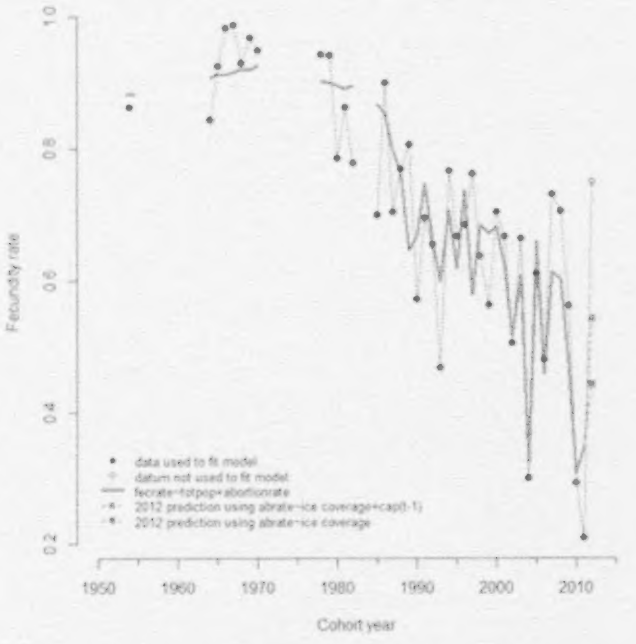

Figure 9. Predictions of the 2012 fecundity rate from the most parsimonious model, using the predicted abortion rates as inputs.

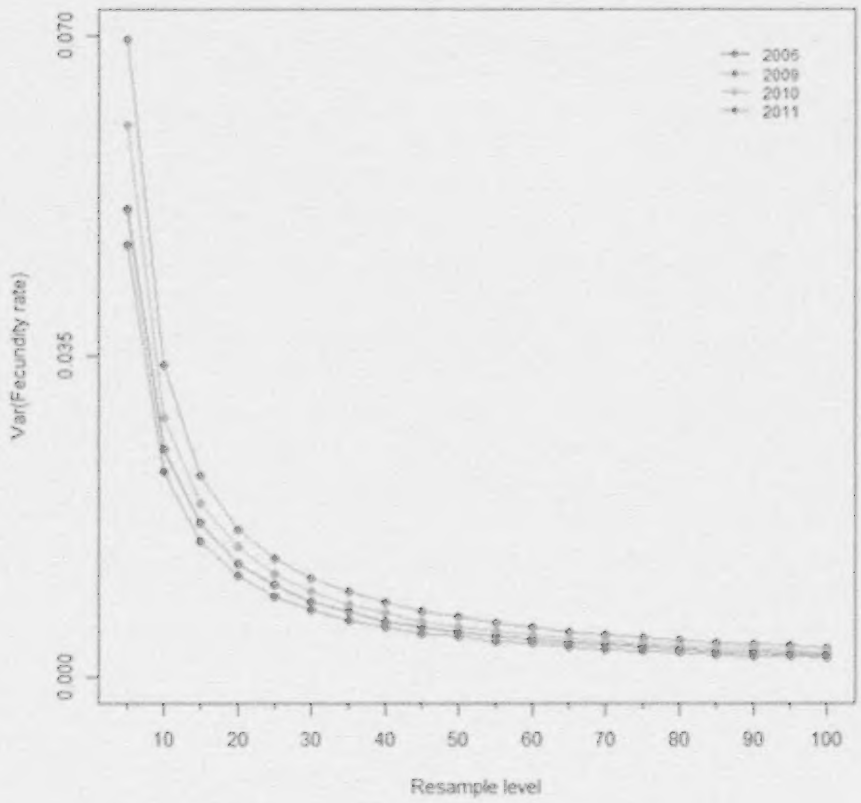

Figure 10. Variance of fecundity rate as a function of bootstrap resampling level. Bootstrap was conducted for years when number of mature animals exceeded 100.